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Genetic and Physiologic Bases For Poultry Improvement

AGRICULTURAL EXPERIMENT STATION
UNIVERSITY OF NEW HAMPSHIRE
DURHAM, NEW HAMPSHIRE

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UNIVERSITY OF NEW HAMPSHIRE
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Genetic and Physiologic Bases for Poultry Improvement

NORTHEAST REGIONAL RESEARCH PUBLICATION

Prepared by the Technical Committee of Northeast Regional Project NE-6, Genetic and Physiologic Bases for Poultry Improvement. A. F. Hicks, Jr., C. S. Shaffner, W. E. Shaklee and J. R. Smyth, Jr., were members of a subcommittee which compiled the report.

Abstract

The NE-6 Regional Poultry Breeding Project began July 1, 1954. The project was a cooperative research effort by poultry scientists of the Northeastern States and was designed to solve some of the basic genetic and physiological problems facing poultry breeders in the region. The project was revised in 1958 and again in 1961 to take into account the progress that had been made. The project was completed in 1963.

Several valuable contributions to poultry breeding research were realized. The development, availability and use of random-bred control populations have been of major importance to poultry breeding research and to the poultry industry. Many of the contributing projects provided new knowledge of basic physiological systems of the domestic fowl including blood pressure, serum and yolk cholesterol, and plasma proteins. Interesting new information was found on plumage color genes and their relationships with other traits. The research on biological selection indexes provided a unique and imaginative approach to multitrait selection. The Regional project stimulated new poultry breeding research and resulted in additional exchanges of ideas and experimental findings among poultry scientists throughout the region. The accomplishments of the project have been published in 36 scientific publications, 16 abstracts and 9 theses.

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Technical Committee Membership

Connecticut (Storrs)	—	J. R. Carson (1954-1958) E. P. Singsen (1959) J. E. Berry (1960-1961) L. D. Matterson (1962) R. G. Somes (1963)
Delaware	—	W. J. Mellen (1954-1957) E. F. Waller (1958) M. S. Cover (1959) P. H. Sammelwitz (1960-1963)
Maine	—	J. R. Smyth, Sr. (1954-1958) J. E. Berry (1959) P. C. Harris (1960-1963)
Maryland	—	C. S. Shaffner (1954-1957) F. H. Wilcox, Jr. (1958-1963)
Massachusetts	—	F. P. Jeffrey (1954) J. R. Smyth, Jr. (1955-1963)
New Hampshire	—	F. L. Cherms, Jr. 1954) W. M. Collins (1955-1963)
New Jersey	—	P. D. Sturkie (1954-1958, 1960-1963) H. S. Weiss (1959)
New York (Cornell)	—	J. H. Bruckner (1954-1963)
Pennsylvania	—	A. J. G. Maw (1954-1956) E. G. Buss (1957-1958) A. F. Hicks, Jr. (1959-1963)
Rhode Island	—	W. K. Durfee (1954-1955) C. D. Gordon (1956) M. R. McClung (1957-1963)
Vermont	—	D. C. Henderson (1960-1963)
West Virginia	—	T. B. Clark (1954-1958) H. M. Hyre (1959-1963)
USDA ARS	—	D. C. Warren (1954-1955) S. C. King (1956-1958, 1960) J. R. Carson (1959) C. W. Hess (1961-1963)
USDA–CSRS	—	R. B. Nestler (1954) W. E. Shaklee (1955-1962) E. C. Miller (1963)
Administrative Adviser	—	W. H. Wiley (1954-1961) A. A. Spielman (1962) R. A. Damon, Jr. (1963)
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Contributing Projects

State	Hatch Project No.	Title	Date Initiated and/or Revised
Conn. (Storrs)	214	The Evaluation of Genetic Relations Among Egg and Meat Production Characters	5/14/54 6/23/58
Conn. (Storrs)	332	Serological Resemblance Among Groups of Chickens as an Aid in Selection	6/20/62
Del.	44-PS	Genetic Differences and Gene-Environment Interactions in Thyroid Activity of Chickens	9/22/54 1/30/57 12/ 6/60
Maine	41	The Relation of Body Size in Poultry to Egg Production and the Growth Rate of Their Progeny	8/16/54
Maine	119	Inheritance of Feed Efficiency and Its Relation to Economic Characteristics of the Chicken	7/ 1/58
Md.	M-33-e	Differences in Thyroid Activity as Related to Strain Differences in Growth, Feed Utilization and Feathering	7/23/54
Md.	M-33-e	Genetic Control of Serum Cholesterol Level	2/ 2/56 1/ 3/58 6/15/61
Mass.	104	Genetic Resistance to Histomonas Meleagridis Infestation in the Turkey	6/29/54
Mass.	178	An Investigation of Possible Pleiotropic Effects of Plumage Color Genes in the Chicken	7/ 1/59
N. H.	92	Selection for General and Specific Combining Ability for Growth Rate	6/17/54
N. H.	92	Recurrent Selection vs Closed Flock Selection for Improving Broiler Qualities	6/13/56
N. H.	137	Recurrent Selection vs Closed Flock Selection for Improving Broiler Qualities in the Crossbred Chicken	6/18/58 7/ 1/60
N. J.	561	Heritability of Blood Pressure in the Fowl	3/ 4/54
N. J.	693	Relationship of Blood Pressure to Health and Productive Performance of Chickens	6/22/61
N. Y.	145	Development and Maintenance of a Random Bred Population of White Leghorns	8/24/54
Pa.	1199-A	Heritability of Certain Egg Quality Characters, the Genetic Correlation Between Them, and the Relation of Such Characters to Reproduction	5/18/54
R. I.	805	The Influence of Selection Against Blood and Meat Spot Incidence Upon Albumen Score	8/10/54 7/ 1/58

Contributing Projects — *(Cont.)*

State	Hatch Project No.	Title	Date Initiated and/or Revised
R. I.	807	The Planning and Coordination of Research Under Regional Project NE-6, Effectiveness of Different Methods of Selective Breeding of Poultry Upon Specific Characters and Associated Characters	8/10/54 7/ 6/56
W. Va.	74	Breeding for Efficient Production of Eggs and Meat	8/16/54
W. Va.	155	Increasing Genetic Variation in Poultry for Selection Purposes Through the Use of Gamma Radiation.	6/ 1/61

Introduction

Poultry and eggs are more important to the agriculture of the Northeastern States than to any of the other 3 geographical regions of the United States. Poultry and eggs are second only to dairy and dairy products as producers of cash farm income in this area.

When NE-6 began in 1954, poultry and eggs accounted for 22% of the realized gross farm income in the Northeast. The area had about 60 million layers on hand which averaged about 195 eggs per layer. The area produced about 290 million broilers and 5.5 million turkeys. Cash farm income from poultry and eggs totaled about $628 million.

When NE-6 closed in 1963, poultry and eggs contributed $644 million of the realized gross farm income to the area. The number of layers on hand had dropped to less than 49 million but egg production per layer had increased to 209. Although turkey production dropped to 4.5 million, broiler production had increased to almost 390 million.

Egg and meat production in the Northeastern States must be maintained at optimum efficiency if profitable poultry enterprises are to continue.

The Regional project was designed to solve some of the basic genetic and physiological problems facing poultry breeders in the Northeastern States.

History

Federal-grant funds for Regional research were authorized with the passage on August 14, 1946 of the amendment to the Bankhead-Jones Act. These Regional research funds were to be used only for cooperative Regional research projects recommended by a committee of nine persons representing the Directors of the State Agricultural Experiment Stations, and approved by the Secretary of Agriculture.

A Regional poultry breeding project was already envisioned in the Northeastern United States. At the December 16-17, 1946 meeting of the Committee of Nine, M. H. Campbell, Director of the Rhode Island Agricultural Experiment Station, was appointed Administrative Advisor to the Northeast Regional Poultry Breeding Project. NE-6 was the number assigned to the project.

However, for financial reasons NE-6 lay dormant for more than seven years. The Northeast Directors at their July 1953 meeting voted to activate NE-6 in view of an expected increase in Regional research funds. By this time Associate Director William H. Wiley of the Rhode Island Agricultural Experiment Station was Administrative Advisor.

Following a Technical Committee meeting January 28-29, 1954, a project outline entitled, "Effectiveness of Different Methods of Selective Breeding of Poultry Upon Specific Characters and Associated Characters." was prepared and accepted. Its objectives were:

1. To develop and evaluate methods for breeding improvement of poultry, especially in egg production, meat production, egg quality, viability, and other economically important factors.
2. To study genetic correlations among economic traits, especially egg production and growth rate.

3. To determine physiology of gene action, especially as reflected by metabolic and endocrine differences in response to selected environmental variables.

4. To study gene-environmental interactions.

The Technical Committee agreed to approach its objectives by each state working on the phase or phases for which it was best equipped.

Priority was given to the development of tester populations under objective 1. An advisory committee on population genetics was appointed and was asked to work out detailed procedures for development and maintenance of randombred control populations. This the advisory committee did at a meeting February 5, 1954.

Don C. Warren was invited to serve as Coordinator in addition to his duties as Coordinator of the other Regional poultry breeding projects.

NE-6 began July 1, 1954 and was revised effective May 1958. The title was shortened to, "Genetic and Physiologic Bases for Poultry Improvement." The objectives were changed to the following:

1. To develop and evaluate methods for breeding improvement of chickens in reproduction, egg quality, meat production. viability and other economically important characters.

2. To determine and evaluate:

   a. Genetic correlations among economic traits.

   b. Genetic bases for differences in physiologic mechanisms.

   c. Gene-environment interactions.

NE-6 was revised a second time effective in April 1961. The title remained the same but the objectives became:

To develop and evaluate methods for use in chicken breeding programs designed to improve reproduction, egg quality, meat production, viability, and other economically important characters. In order to accomplish this goal, it is necessary to determine and evaluate the following:

1. Genetic bases for differences in physiological mechanisms.

2. Genetic parameters for economic traits.

3. Gene-environment interactions.

NE-6 was terminated in June 1963. Procedures and results are summarized in the following paragraphs. More detailed information may be found in the publications listed at the end of the bulletin.

Procedure

The organization and supervision of the cooperative project was in the hands of the Regional Technical Committee. The Committee consisted of a Director of an Agricultural Experiment Station in the region acting as the Administrator Advisor, one representative of each of the cooperating Agricultural Experiment Stations, a representative of the

Animal Husbandry Research Division, Agricultural Research Service, USDA, and a non-voting member representing the Cooperative State Research Service, USDA.

The Regional Technical Committee came together for a meeting each year to discuss progress and problems and to coordinate plans for future research.

Each of the State Agricultural Experiment Stations in the Northeast was invited to appoint a representative on the Technical Committee. Each representative doing research on the Regional project prepared a contributing project outline covering his contribution to the Regional effort. As progress was made and objectives changed, many of the contributing projects were revised to recognize the new direction of the research. A list of the individual contributing projects is provided on pages 4 and 5.

Results

A. BREEDING METHODS

Poultry breeders are constantly on the alert for new methods which will permit more rapid progress in breeding for increased egg and meat production. The first objective of NE-6 was to develop and evaluate methods for breeding improvement of poultry, especially in egg production, egg quality, meat production, viability and other economically important factors.

However, in order to evaluate adequately different breeding methods, control populations were considered necessary. The Technical Committee decided to develop randombred populations of chickens for use as controls.

Randombred Populations

Poultry geneticists have long felt a need of a system whereby genetic progress could be measured from one year to another. Environmental fluctuations often made it impossible to determine if changes which occurred from year to year had a real genetic basis. To solve this problem, two randombred control populations of chickens with broad genetic origins were originated to assist in fulfilling the objectives of NE-6 (3, 26). In addition to the function of providing genetically stable flocks, the randombred populations served as useful bases for the initiation of selection experiments.

Maintenance procedures were designed to minimize those factors which change gene frequency. Each population was maintained with no less than 50 male and 250 female breeding birds and no full or half sibs were permitted to mate. Also, each sire was permitted only one son and each dam only one daughter as breeders in the next generation.

The heavy breed Connecticut randombred population was formed by a double cross of four strains of Columbian-patterned birds (2). It was designed to contain a sampling of genes from both egg and meat strains. Numerous traits, such as rate of feathering, feather color, feather pattern, stubs, side sprigs, and ear lobe color, were recorded in each generation so that genetic stability could be estimated.

The light breed Cornell randombred population was produced from commercial strain crosses of White Leghorns from several different sources. Every chick hatched in the first generation had at least four different high producing White Leghorn strains in its background. Later, hatching eggs from the Cornell randombred population were supplied to the North Central Regional Poultry Breeding Laboratory at Lafayette, Indiana. This made the population available to the NC-47 Regional project, and made it feasible to study possible genetic changes in the two flocks maintained under two different environments. Also, the possibility of a disastrous loss of the population was reduced.

The randombred control populations have been used in the NE-6 Regional project to measure genetic progress in the different contributing projects. They have also been used in nutrition and physiology experiments where a broad genetic base was needed. They have been highly valued in providing genetically stabilized flocks for use as environmental control flocks at many experiment stations and random sample poultry tests, for the estimation of genetic parameters in unselected populations, and for foundation flocks in directional selection experiments. Tables I, II and III provide heritabilities, genetic correlations and phenotypic correlations of various traits estimated from these and other poultry populations in NE-6 (27, 56).

The Cornell randombreds have been widely used as experimental material in the United States and are now maintained at the North Central Regional Poultry Breeding Project at Lafayette, Indiana. Samples of hatching eggs from these and other light breed randombred controls are available from the North Central project for experimental work. The Connecticut randombred population has been discontinued but other heavy breed randombred controls are maintained at the Southern Regional Poultry Genetics Laboratory at Athens, Georgia.

Mass Selection

A 10-year mass selection experiment was conducted at the Reymann Memorial Farms substation of the West Virginia Agricultural Experiment Station (25). The birds were pen-pedigreed only, and selection was based on individual 10-week body weights and breast angle measurements. A non-selected line was maintained as a control.

Mass selection was effective in increasing both traits in comparison with the control. The rate of increase was consistent with the genetic theory of selection.

Crossbreeding

Earlier research had shown that crossbreeding was advantageous for producing broilers. However, reproduction in meat type stocks left much to be desired. Researchers at the West Virginia Agricultural Experiment Station approached this problem by crossing meat type New Hampshires with high egg producing White Leghorns, Rhode Island Reds and Barred Plymouth Rocks (9, 25). The F_1 crossbred females were then mated to meat type Dominant White males to produce the broiler chicks.

Almost without exception, the F_1 females produced more eggs than

either of the parent stocks. The highest production was from progeny of Rhode Island Reds crossed with New Hampshires.

Good broilers were produced by F_1 females mated to Dominant White males. However, their growth rate to 10 weeks of age was not as good as the progeny of New Hampshire females mated to Dominant White males.

Recurrent Selection

A test was made at the New Hampshire Agricultural Experiment Station of recurrent versus closed flock selection for improving broiler qualities in the crossbred chicken (38, 40). A cross line progeny test showed no advantage over a pure line progeny test for improving 8-week body weight within a line. Crossbred progeny of 4th generation males from the two selected lines mated to randombred females were heavier from the recurrent line than from the closed line, but the difference was not significant.

Diallel Matings

Additive genetic variance, in contrast to non-additive genetic variance such as dominance and epistasis, is most readily utilized in selective breeding programs. It is desirable, therefore, to know the proportion of the total genetic variance in a trait which may be attributed to genes acting additively. Component estimates of non-additive genetic variance for 8-week body weight were obtained from a diallel mating experiment at the New Hampshire Agricultural Experiment Station. The test, which was replicated over two years with two groups of birds, gave estimates of non-additive genetic variation which were not significant. Thus, non-additive genetic variation was not an important fraction of the total variation in body weight, but it could have some small influence on it.

Gamma Irradiation

The effect of gamma irradiation of New Hampshire fowl semen on ten-week body weight, mortality, egg production, egg weight, fertility and hatchability was studied at the West Virginia Agricultural Experiment Station. The semen of the irradiated line was subjected to a total dose of 1,500 roentgens of gamma irradiation at a dose rate of 3,600 roentgens per hour. Selection of breeding stock for subsequent generations was based entirely on ten-week body weight and data were collected for two generations.

The irradiation of the semen did not affect ten-week body weight, egg production or mortality to ten weeks of age. Egg size in the irradiated line was found to be less than that for the non-irradiated line, and fertility and hatchability were both reduced by the treatment.

Summary

A critical review indicates that NE-6 was moderately successful in attaining the first objective of developing and evaluating methods for breeding improvement of poultry.

The development of randombred control populations was the most

important contribution to this objective in that it provided a stable base for other research.

Mass selection was effective in increasing 10-week body weights and breast angle measurements in meat type birds. Crossbreeding was effective in improving reproductive performance in broiler stocks but growth rate to 10 weeks of age suffered in the process. Recurrent selection showed no advantage over closed flock selection in broiler stocks.

In the absence of a significant amount of non-additive genetic variation in 8-week body weight, conventional breeding methods should be effective in improving the trait. The production of genetic variation by the irradiation of sperm was not a useful adjunct to selective breeding for the improvement of ten-week body weight.

B. GENETIC CORRELATION AND SELECTION RESPONSE

The second objective of NE-6 was to study genetic correlations among economic traits, especially egg production and growth rate.

Poultry breeders have long been aware that selection for superiority of one economic trait may result in correlated responses in other traits. The association between body weight and egg weight demonstrates a positive correlated response. On the other hand, selection for egg production was often accompanied by reduced growth rate. Genetic correlations were estimated from randombred and other populations and were observed in selection experiments.

It is important that we know which traits are genetically related to which other traits and the direction and magnitude of these relationships. Such knowledge can be used in breeding programs to make optimum progress in all the important economic traits. A summary of genetic correlations estimated from research in NE-6 is given in Table II.

Biological Selection Indexes

The problem of correlated responses to selection and of measuring the aggregate phenotype of chickens was investigated by the formulation of biological selection indexes and the theoretical evaluation of their use as selection criteria as compared with the consequences of selection for single traits. Directional selection for a single trait may result in compensatory regression of other traits. By the use of biological selection indexes a balance of traits can be found which allows the maximum increase in the most desirable traits without sacrificing other characteristics of economic value.

At the Pennsylvania Agricultural Experiment Station, egg number, average egg weight, and body weight were measured (21, 22). The term, biomass, was applied to these three traits considered together, while the term, egg mass, was applied to egg number and egg weight. It was found that egg mass used as a single criterion of selection would reduce age at sexual maturity, increase egg number, increase specific gravity of the eggs, increase reproductive potential, increase body weight only slightly, and leave egg weight practically unchanged.

Offspring from four lines of New Hampshires at the West Virginia Agricultural Experiment Station were weighed and measured for breast angle at 10 weeks and at 6 months of age (10). Phenotypic correlations

between the two traits were 0.29 at 10 weeks and 0.27 at 6 months of age. Heritability estimates of body weight and breast angle at 10 weeks averaged 50 and 30 percent, respectively, and at 6 months 40 and 25 percent. Selection indexes were constructed from these data. The weighting factors determined for the indexes were designed to obtain maximum progress in both traits.

Blood Pressure

Researchers at the New Jersey Agricultural Experiment Station developed an improved method of measuring systolic blood pressure in chickens (50). The new method involved a compact, portable and relatively inexpensive unit which could be easily attached to the bird's shank while in an upright position.

Selection of lines for high and low systolic blood pressures of White Leghorns resulted in differences between lines after the first generation of selection (55). Cardiac output and stroke volume of hypotensive females were greater than of hypertensive females. However, this did not occur in males. Total peripheral resistance of hypertensive birds of both sexes was greater than that of hypotensive birds and in females the difference was even more striking. Heart rate of the two lines did not differ (53, 54).

Mortality was greater in both sexes of the low blood pressure line than in the high blood pressure line. This was also true in unselected birds, but the difference in mortality became less when total mortality was low (51). A similar situation was found with respect to the abilities of the birds of the selected lines to withstand exercise stress (52). In general, the biological efficiency of the birds was better in the high pressure line than in the low pressure population.

Meat Spots

Data were analyzed from 6 generations of selection for low meat spot incidence in a Rhode Island Red line at the Rhode Island Agricultural Experiment Station (31, 32). The number of eggs free of meat spots was increased by 8.7% per generation. The realized heritability of meat spots was 0.68. This undesirable trait was virtually eliminated from the line. The percentage of hens laying meat-spot free eggs increased from none in the zero generation to 37% in generation six.

However, as the percent of eggs free of meat spots increased, the percent hen-day production decreased by 2.84% per generation. This negative correlated response was significant. Also, a reduction in shell thickness occurred. Correlated responses to percent incidence of meat spots were not detected for age at first egg, egg weight, blood spot incidence, Haugh units or albumen height. There were no significant changes in the magnitude of the selection differentials during the experiment.

The population was later mated at random and one group of eggs were stored for 24 hours, another for 12 days at 50 to 55°F. Heritability of albumen height differences after storage (fresh eggs minus stored eggs for each bird) was estimated. Heritability estimated from the dam component was 4% at 8 months of age and 18% at 12 months of age. Estimates from sire components were negative at both ages (30).

Serum Cholesterol

An experiment was undertaken at the Maryland Agricultural Experiment Station to determine the influence of age during the growing period on levels of serum cholesterol (6). The chicks were from a cross between White Leghorn males and females of a flightless strain of domestic fowl. Although serum cholesterol at hatching time was higher by 3 times than at any other time from 1 to 10 weeks of age, the age variation was not significant.

Differences in serum cholesterol level among dam-families were found when measured in the Cornell randombred population of White Leghorns at 6 to 9 weeks of age (4, 5). Heritability of the trait was estimated to be 0.30.

After 5 generations of selection the low line was greater than the high line in 6 week body weight, while the Haugh units of the high line exceeded those of the low line. The lines did not differ in adult body weight, mortality, fertility, hatchability, egg weight, specific gravity of eggs, egg production, or egg yolk cholesterol (59).

When the high and low lines were crossed after 5 generations of selection, the average cholesterol levels in reciprocal crosses were close to each other and to the average of the two lines. After 6 generations of selection, the cholesterol level of the high line was approximately 30% greater than that of the low line. Liver synthesis of cholesterol was equivalent in the two lines but fecal excretion of the metabolite was greater in the low line (7, 8).

Correlations were calculated between serum cholesterol of 6 week old chicks and adults and ten other traits (58). The only repeatable and significant phenotypic correlations of serum cholesterol of adult birds were with serum cholesterol at 6 weeks of age (+0.13), egg weight (—0.13 in October and —0.18 in March) and albumen quality (—0.24 in October and —0.22 in March). Genetic correlations of serum cholesterol in young pullets were positive for chick body weight, age at first egg, egg production and albumen quality but were negative for adult body weight.

Summary

Much new information was obtained under the second objective of studying genetic correlations. The research on biological selection indexes provide a new and imaginative approach to multitrait selection. The estimates of heritability and genetic correlations developed in the project provided bases for new selection indexes designed to maximize overall genetic progress in selection.

The blood pressure selection project resulted in much new information of interest to the medical profession as well as to poultry physiologists. The biological efficiency of the high blood pressure line was better than of low pressure birds. The meat spot selection project demonstrated that this undesirable trait can be easily reduced to an insignificant level in a population but egg production and egg shell thickness decreased at the same time. Selection for high serum cholesterol resulted in higher Haugh units but lower 6-week body weight than selection for low serum cholesterol.

C. INDIVIDUAL TRAIT ANALYSIS AND THE PHYSIOLOGY OF GENE ACTION

The third objective of NE-6 was the analysis of individual traits and to interpret the type of gene action involved with special reference to metabolic and endocrine effects.

Genes produce their effects in many ways. Some genes affecting plumage color, for example, seem to produce large and dramatic primary effects simply and directly. On the other hand, some traits such as egg production seem to be influenced by many genes, each of which has small effects which in turn may be mediated through the endocrine system or other physiological pathways. Several contributing projects to NE-6 were directed toward this third objective.

Plasma Proteins

In four separate trials of 27 to 30 birds each, plasma proteins of individual female chickens from the Connecticut randombred population were separated into 15 fractions by researchers of the Connecticut Agricultural Experiment Station (41). Analyses of total protein or levels of the 15 protein fractions with five economic traits showed no consistent correlations. However, analyses between total protein or levels of the 15 protein fractions and four indices describing state of productivity near the time of blood collection did show consistent correlations. Protein components F and G repeatedly showed close relationships with all four indices of productivity (number of days since last egg, seven-day production before bleeding, 14-day production before bleeding, and seven-day production before and after bleeding). Also, a relationship was suggested between the amount of component L and some of the productivity measurements. These data suggest a functional relationship between some of the chromatographically distinct plasma protein components and the short term dynamic and complex metabolic systems concerned with egg productivity.

Plumage Color

Some genes which primarily determine feather colors and patterns influence other traits as well, i.e., their action is pleiotropic. At the Massachusetts Agricultural Experiment Station populations homozygous for recessive white were established which were segregating for alternate alleles at five different loci. The use of suitable testing procedures revealed that the gene *E* was associated with greater mortality, including more leucosis, than its allele e^{b} for three consecutive generations. Birds possessing the genotype Ii^{+} or Ee^{b} were superior to their $i^{+}\ i^{+}$ flockmates with respect to survivor egg production and to hen-caged egg production for several generations. However, this relationship disappeared after the F_5 generation.

In another experiment designed to examine pleiotropic effects of plumage color genes, it was found that colored birds ($C^{+}c$) were heavier at 8 weeks of age than their recessive white sibs (cc) (48, 49). When the $C^{+}C^{+}$ and $C^{+}c$ genotypes were compared with cc genotypes, the results indicated no superiority for either the heterozygote or the homozygous dominant group. It was not determined whether these results

were due to close linkage with growth rate genes, or to a true pleiotropic effect of the $C+$, c alleles.

Social and sexual behavior were studied in Fayoumi fowl in which the alleles for the presence or absence of autosomal barring were segregating (11, 12). When the two types of birds were reared intermingled, white females were socially dominant to barred females, but when reared separately, barred females were dominant to their white counterparts when intermingled as adults. No consistent differences in mating behavior were found. The socially dominant group consistently laid more eggs than the subordinate group.

Phaeomelanin intensity was studied in feathers of Buff Orpington, New Hampshire and Rhode Island Red chickens (43, 44, 45, 46, 47). Phaeomelanin intensity of chick down feathers was correlated with that of post-juvenile feathers (44). A correlation was also found between postjuvenile and adult feathers in females. Correlations were high between postjuvenile and adult feathers in males. Feathers from sex-linked slow feathering (K) females contained more phaeomelanin than those from their rapid feathering ($k+$) sibs. A series of appropriate matings demonstrated that phaeomelanin intensity was a quantitatively inherited trait. No evidence for sex-linkage was found. The phaeomelanin was fractionated into three parts, brown, purple I and purple II. All three fractions were shown to be genetically controlled.

Shank Pigmentation

Yellow shank color observations were recorded at the New Hampshire Agricultural Experiment Station (39). Scores ranged from 1 (lightly pigmented) to 5 (deeply pigmented) on 10 week old birds. The experimental birds were progeny of a cross of dominant white meat type males mated to Columbian patterned meat type females.

Shank color score ranged from 2.1 to 3.7 among males and from 1.2 to 3.3 among females. The data suggested the existence of real sire differences for shank color, and sex-linked genes seemed to be involved. Heritability of this trait estimated from the sire component was 0.53 averaged for both sexes while the sire plus dam components averaged 0.41.

In another experiment at the New Hampshire Station shank color scores were taken at 8 weeks of age from two meat type lines (61). Average color scores of males from the 2 lines ranged from 1.6 to 2.4 in both 1960 and 1961. In females the scores ranged from 1.4 to 1.9. Heritability estimates among male progeny were 0.21 from the sire component and 0.69 from the dam component. Among female progeny the estimates were 0.16 and 0.23, respectively. The genetic correlations between shank pigmentation and body weight at 8 weeks of age were consistently negative.

Thyroid Activity

Several techniques for measuring the thyroid activity of chickens were studied at the Delaware Agricultural Experiment Station. The objective was to find a reliable index of thyroid activity for a variety of physiological and genetic studies with domestic fowl. A good measure

of thyroid activity was needed before metabolic rate could be modified by genetic selection.

The level of circulating protein bound iodine was not a satisfactory measure of thyroid gland activity in the fowl (34).

In vivo changes in the I^{131} content of the thyroid gland were estimated by giving graded doses of pure L-thyroxine (37). The birds were fed thiouracil to minimize reutilization of I^{131} from metabolized hormone. This method was useful for group comparisons but not for individual birds. One *in vivo* technique using I^{131}, thiouracil, and replacement thyroxine was effective in discriminating individual differences. However, it was considered too complex for routine use.

The technique of measuring, *in vitro*, the red blood cell uptake of radioiodinated triiodothyronine was found to be inappropriate in chickens.

The relative potencies of L-thyroxine and of L-triiodothyronine in reducing thyrotrophic hormone secretion were determined by the radioiodine method and by goiter-prevention assay (35, 36). Although L-triiodothyronine had been shown to be several times as effective as L-thyroxine in mammals, this was not true in chicks. In fact, L-thyroxine was somewhat more potent in chicks.

Thyroprotein and thiouracil were fed to young White Leghorn chickens to investigate the metabolic rate as measured by oxygen consumption (33). Results depended largely upon the fasting period prior to metabolic rate determinations. Metabolic rate was depressed by thiouracil for 18 hours after the drug was withheld after which it returned to normal. Metabolic rate was stimulated by thyroprotein only a few hours after the drug was withheld.

The relationship of metabolic rate to body size was investigated. It was concluded that either the use of a regression adjustment for individual animal data or the $\frac{3}{4}$ power of body weight gave a reasonably good correction for differences in body size.

Yolk Cholesterol

Egg yolk cholesterol was measured at the Maryland Agricultural Experiment Station in a sample from the Cornell randombred control population of Single Comb White Leghorns (16, 17, 18, 19, 20). Significant differences among individual hens were found but no differences due to sire or dam were detected. The cholesterol level was expressed as mg. cholesterol per gram of yolk on a wet basis. Yolk cholesterol of eggs laid in November was phenotypically correlated with egg weight (0.19), specific gravity (0.27) and yolk cholesterol of eggs laid by the same hens the following March (0.32). A negative correlation was found between egg yolk cholesterol and yolk weight (–0.15). Yolk cholesterol was not correlated with serum cholesterol, age at first egg, egg production, body weight or albumen quality. Egg yolk cholesterol varied with season. The concentration of cholesterol increased from 25.1 milligrams per gram of yolk in August to 26.1 in February after which it decreased to 25.3 in June.

The feeding of crystalline cholesterol to Single Comb White Leghorns of a commercial strain resulted in an increase in yolk cholesterol of almost 50%. The increase in serum cholesterol ranged from 30 to

38%. However, this increase was not significant, suggesting that laying hens prevent a marked hypercholesterolemia by excreting it in the yolk.

Embryo Weight

At the New Hampshire Agricultural Experiment Station, controlled matings were made from meat-type chickens previously selected for 8-week body weight (60). Hatching eggs were incubated and the embryos were weighed 14 days later. Significant line and sire differences in 14 day embryo weights were found.

Feed Efficiency

Studies of the efficiency of feed utilization for egg production were conducted at the Maine Agricultural Experiment Station. Distinct possibilities were revealed for the selective improvement of the trait. Heritability estimates were in the range of 30 to 50% when feed utilization figures were corrected for egg mass, body weight, and body weight changes during the test period.

Immunogenetics

When rabbits were immunized to chicken blood at the Connecticut Agricultural Experiment Station, a difference was found in the reaction of rabbit antisera to the blood plasma of New Hampshire, Rhode Island Red, Leghorn and Cornish chickens (1). However, individual chickens of the same breed could not be distinguished on the basis of their plasma antigens with the techniques used.

Summary

The greatest activity in NE-6 was on the third objective of determining the physiology of gene action and much progress was made.

In a study of 14 day embryo weight, important line and sire differences were described. A feed efficiency study revealed highest heritability estimates when the data were corrected for egg mass, body weight, and body weight changes during the test period. Different breeds of domestic fowl were found to differ in their plasma antigens and some protein components repeatedly showed close relationships with short term egg production.

Several interesting relationships of plumage color genes with other traits were noted. The gene for extension of black pigmentation was associated with high mortality, dominant white birds had superior egg production, colored birds were heavier at 8 weeks of age than recessive white birds, and autosomal barring was associated with social dominance. Yellow shank pigmentation was shown to have medium to low heritability. Considerable difficulty was encountered in searching for a good measure of thyroid gland activity. Egg yolk cholesterol was a highly variable trait easily influenced by diet and season, and no sire or dam influences could be detected.

D. GENE-ENVIRONMENTAL INTERACTIONS

The fourth objective was to study gene-environmental interactions.

Poultry breeders have long suspected that strains bred in one geographical location or under specific conditions would not perform equally well in other locations or under other conditions. The use of randombred populations as controls at the different State experiment stations in the region provided an opportunity to evaluate gene-environmental interactions.

Nutritional Environment

Single Comb White Leghorns at the Pennsylvania Agricultural Experiment Station were fed two different layer-breeder diets. The rations were isocaloric but the level of nutrients in one was approximately 80% of that of the other (23). The data were analyzed for survivors egg number for 10 months. The dominance and maternal variance as a proportion of the additive genetic variance was more than 10 times as high for the high ration as for the low ration. The sire component estimate of heritability was 10% for the high ration and 28% for the low. These results indicate that selection for total egg production on the low diet would be superior to high ration selection regardless of the ration used for the progeny.

Raising Sexes Separately

Two trials using chicks from a commercial broiler cross were studied at the New Hampshire Agricultural Experiment Station (29).

Contrary to some reports, raising sexes separately did not reduce the variation in 9-week body weight below that observed for each sex when both sexes were brooded together. The coefficients of variation were larger for males brooded separately than for those brooded mixed, but for females the relationship was reversed.

Randombred Populations

The first 6 years of data collected from the Cornell randombred control population were analyzed for nine different traits (27). Year to year variability was found but no trends were evident. Estimates of heritability from this and other studies in NE-6 are given in Table 1. Maternal effects accounted for 13% of the total variance in egg production. Maternal effects also were important for 8, 32 and 55-week body weight and for sexual maturity.

In another analysis Cornell and USDA workers used data for eight economic traits from the Cornell randombred control populations maintained at Ithaca, New York and Lafayette, Indiana (56). Most estimates of the variation due to genetic-environmental interaction were small. The three largest estimates were 9% for egg production, 8% for 8-week body weight and 6% for 32-week egg weight. As in the previous study, the variation due to maternal effects was relatively large for sexual maturity and egg production. The sire effects were small. These results suggest the need for a reappraisal of breeding programs for these traits with more investigations on methods of capitalizing on the maternal effects.

Effects of season on egg quality traits were studied in a randombred flock of S. C. White Leghorns at the Pennsylvania Agricultural Experiment Station (24). For the purpose of this study, the data from 4 years were grouped into period one (December and January), period two (February), period three (March and April) and period four (June). Egg weight and egg shape increased from period one to period two and then stabilized. Haugh units and shell thickness declined consistently from period to period with the maximum decrease occurring in the spring.

Summary

The few projects undertaken in NE-6 on gene-environmental interactions were quite successful.

A low plane of nutrition provided higher estimates of additive genetic variance and heritability for survivors egg number than did a high plane of nutrition.

Raising sexes separately had little effect on variation in 9-week body weight. In the Cornell randombred control populations, the variation due to genetic-environmental interactions was small. The largest estimates were 9% for egg production, 8% for 8-week body weight and 6% for 32-week egg weight.

Conclusions

Although the objectives of NE-6 were not completely and clearly attained in detail, a number of important contributions to poultry breeding research may be cited.

1. The development, availability and use of randombred control populations have been of major importance to poultry breeding research and to the poultry industry.

2. Many of the contributing projects provided new knowledge on basic physiological systems of the domestic fowl.

3. The research on biological selection indexes provides a unique and imaginative approach to multitrait selection.

4. The 36 scientific publications, 16 abstracts, and 9 theses that evolved from the project represent a significant record of research productivity.

5. The NE-6 project has provided an unusual stimulus to poultry breeding research in the Northeast. The annual meeting of researchers with different backgrounds of training and experience but with common goals has resulted in fertile exchanges of ideas to the mutual benefit of all concerned.

6. Finally, the cooperative nature of the research has made results from one or more states readily known and available to workers in the entire region. In this way the poultry industry of the Northeast has benefited much more than would normally be expected.

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Table I. Heritability Estimates

Trait	Heritability Percent	Method of Estimation	Station
Age at Maturity	7	Sire Comp.	New York
" " "	9	" "	" "
" " "	34	Dam "	" "
" " "	45	" "	" "
Albumen Score	25	Sire "	" "
" "	29	" "	" "
" "	6	Dam "	" "
" "	40	" "	" "
Blood Pressure	28	Parent-Offspring Regr.	New Jersey
Blood Spot Score	13	Sire Comp.	New York
" " "	28	Dam "	" "
Body Wt. of Males — 4 Wk.	20	Sire "	New Hampshire
" " " "	76	Dam "	" "
" " Females "	26	Sire "	" "
" " " "	90	Dam "	" "
" " Males 6 Wk	26	Sire "	" "
" " " "	75	Dam "	" "
" " Females "	31	Sire "	" "
" " " "	75	Dam "	" "
" " Males 8 Wk.	24	Sire "	" "
" " " "	66	Dam "	" "
" " " "	39	Sire "	" "
" " " "	52	Dam "	" "
" " Females	35	Sire "	" "
" " " "	22	" "	New York
" " " "	29	" "	" "
" " " "	76	Dam "	New Hampshire
" " " "	37	Sire "	" "
" " " "	53	Dam "	" "
" " " "	35	" "	New York
" " " "	69	" "	" "
" " " 10 Wk.	50	Intrasire Regr.	West Virginia
" " " 6 Mo.	40	" "	" "
" " " 32 Wk.	43	Sire Comp.	New York
" " " "	48	" "	" "
" " " "	73	Dam "	" "
" " " "	89	" "	" "
" " " 55 Wk.	44	Sire "	" "
" " " "	76	Dam "	" "
Breast Angle " 10 Wk.	30	Intrasire Regr.	West Virginia
" " " 6 Mo.	25	" "	" "
Embryo Weight — 14 Days	18	Sire Comp.	New Hampshire
Egg Production — Hen Housed	0	" "	New York
" " " "	7	" "	" "
" " " "	60	Dam "	" "
" " " "	59	" "	" "

Table I. Heritability Estimates *(Cont.)*

Trait	Heritability Percent	Method of Estimation	Station
Egg Shape	37	Intrasire Regr.	Pennsylvania
" "	52	" "	"
" "	30	" "	"
" "	41	" "	"
Egg Weight	33	" "	"
" "	16	" "	"
" "	14	" "	"
" "	16	" "	"
" " 32 Wk.	51	Sire Comp.	New York
" " "	72	" "	" "
" " "	64	Dam "	" "
" " "	42	" "	" "
" " 55 Wk.	53	Sire "	" "
" " "	67	" "	" "
" " "	58	Dam "	" "
" " "	41	" "	" "
Feed Efficiency	76	Intrasire Regr.	Maine
" "	23	" "	"
" "	46	Full-Sib	"
" "	36	" "	"
Haugh Units	24	Intrasire Regr.	Pennsylvania
" "	2	" "	"
" "	11	" "	"
" "	8	" "	"
Meat Spot Score	68	Realized	Rhode Island
Serum Cholesterol Level	19	Sire Comp.	Maryland
" " "	34	" "	"
" " "	30	Full-Sib	"
" " "	25	" "	"
Shank Pigmentation (10 wk.)	53	Sire Comp.	New Hampshire
" " "	41	Full-Sib	" "
" " Males (8 wk.)	21	Sire Comp.	" "
" " " "	69	Dam Comp.	" "
" " Females "	16	Sire Comp.	" "
" " " "	23	Dam Comp.	" "
Shell Thickness	23	Intrasire Regr.	Pennsylvania
" "	6	" "	"
" "	32	" "	"
" "	8	" "	"
Specific Gravity Score	34	Sire Comp.	New York
" " "	30	" "	" "
" " "	6	Dam Comp.	" "
" " "	33	" "	" "

Table II. Genetic Correlations

Correlated Traits	Correlation	Station
Body Weight at 8 weeks and		
Body weight at 32 weeks	0.71	New York
Age at maturity	— 0.17	" "
Egg production	0.20	" "
Egg weight at 32 weeks	0.32	" "
" " " 55 "	0.34	" "
Albumen score	— 0.01	" "
Blood spot score	— 0.09	" "
Specific gravity score	— 0.01	" "
Body weight at 32 weeks and		
Age at maturity	0.00	" "
Egg production	0.04	" "
Egg weight at 32 weeks	0.32	" "
" " " 55 "	0.30	" "
Albumen score	0.01	" "
Blood spot score	0.13	" "
Specific gravity score	0.09	" "
Age at Maturity and		
Egg production	— 0.44	" "
Egg weight at 32 weeks	0.18	" "
" " " 55 "	0.16	" "
Albumen score	— 0.07	" "
Blood spot score	— 0.09	" "
Specific gravity score	0.06	" "
Egg Production and		
Egg weight at 32 weeks	— 0.04	" "
" " " 55 "	— 0.01	" "
Albumen score	0.04	" "
Blood spot score	0.01	" "
Specific gravity score	— 0.07	" "
Egg Weight at 32 weeks and		
Egg weight at 55 weeks	0.98	" "
Albumen score	— 0.14	" "
Blood spot score	0.01	" "
Specific gravity score	0.06	" "
Egg Weight at 55 weeks and		
Albumen score	— 0.11	" "
Blood spot score	— 0.01	" "
Specific gravity score	0.04	" "
Albumen Score and		
Blood spot score	0.02	" "
Specific gravity score	0.05	" "
Blood Spot Score		
Specific gravity score	— 0.27	" "

Table II. Genetic Correlations *(Cont.)*

Correlated Traits	Correlation	Station
Meat Spot Incidence and		
Egg shell thickness	— 0.43	Rhode Island
Egg weight	— 0.04	" "
Albumen height	— 0.16	" "
Haugh units	— 0.19	" "
Egg production	0.01	" "
Shank Score and		
Body weight at 8 weeks		
Males	— 0.65	New Hampshire
Females	— 0.44	" "
Serum Cholesterol (6 wk.) and		
Body weight at 8 weeks	0.37	Maryland
Adult body weight	— 0.37	"
Age at first egg	0.33	"
Egg production	0.37	"
Egg weight (Oct.)	0.09	"
" " (Mar.)	0.35	"
Albumen quality	0.23	"
Blood spot incidence	0.00	"
Meat spot incidence	0.00	"
Shell strength	0.00	"

Table III. Phenotypic Correlations

Correlated Traits	Correlation	Station
Body Weight at 8 weeks and		
Body weight at 32 weeks	0.54	New York
Age at maturity	— 0.04	" "
Egg production	0.04	" "
Egg weight at 32 weeks	0.21	" "
" " " 55 "	0.24	" "
Albumen score	— 0.02	" "
Blood spot score	0.01	" "
Specific gravity score	0.01	" "
Body weight at 32 weeks and		
Age at maturity	0.08	" "
Egg production	0.15	" "
Egg weight at 32 weeks	0.41	" "
" " " 55 "	0.40	" "
Albumen score	— 0.02	" "
Blood spot score	0.00	" "
Specific gravity score	— 0.01	" "

Table III. Phenotypic Correlations *(Cont.)*

Correlated Traits		Correlation	Station
Age at first egg and			
Egg production		— 0.20	" "
Egg weight at 32 weeks		0.04	" "
" " " 55 "		0.03	" "
Albumen score		— 0.03	" "
Blood spot score		— 0.01	" "
Specific gravity score		0.03	" "
Egg Production			
Egg weight at 32 weeks		0.00	" "
" " " 55 "		— 0.03	" "
Albumen score		0.04	" "
Blood spot score		0.00	" "
Specific gravity score		— 0.04	" "
Egg Weight at 32 weeks and			
Egg weight at 55 weeks		0.68	" "
Albumen score		— 0.06	" "
Blood spot score		0.01	" "
Specific gravity score		0.02	" "
Egg Weight at 55 weeks and			
Albumen score		— 0.05	" "
Blood spot score		0.00	" "
Specific gravity score		0.00	" "
Albumen Score and			
Blood spot score		0.00	" "
Specific gravity score		— 0.08	" "
Blood spot score and			
Specific gravity score		0.00	" "
Body weight at 10 weeks and			
Breast angle at 10 weeks		0.29	West Virginia
Body weight at 6 months and			
Breast angle at 6 months		0.27	" "
Postjuvenile feather color and			
Adult feather color (optical density)			
Buff Orpington	male	0.92*	Massachusetts
New Hampshire	"	0.82*	"
Rhode Island Red	"	0.77*	"
NH x BO — F_1	"	0.88*	"
RIR x BO — F_1	"	0.70*	"
NH x RIR — F_1	"	0.76*	"
Buff Orpington	female	0.64	"
New Hampshire	"	0.53*	"
Rhode Island Red	"	0.80*	"
NH x BO — F_1	"	0.63	"

Table III. Phenotypic Correlations *(Cont.)*

Correlated Traits		Correlation	Station
RIR x BO — F_1	female	0.88*	"
NH x RIR — F_1	"	0.68*	"
Chick down feather color and postjuvenile feather color			
Among purebreds		0.95*	"
Among F_1 crosses		0.95*	"
Among F_2 crosses		0.96*	"
November yolk cholesterol and			
Serum cholesterol (6 wks.)		— 0.03	Maryland
" " (25 wks.)		— 0.03	"
Age at first egg		0.16	"
Egg production (Oct.-Dec.)		— 0.17	"
Body weight (March)		0.15	"
Egg weight		0.19*	"
Specific gravity		0.27*	"
Haugh units		0.07	"
March yolk cholesterol and			
Novembebr yolk cholesterol		0.32*	"
Serum cholesterol (6 wks.)		— 0.08	"
" " (25 wks.)		— 0.06	"
Age at first egg		— 0.12	"
Egg production (Oct.-Dec.)		— 0.17	"
Body weight (March)		0.13	"
Egg weight		— 0.08	"
Specific gravity		0.21	"
Haugh units		0.07	"
Yolk weight and			
Yolk cholesterol (Nov.)		— 0.17*	"
" " (March)		— 0.09	"
" " (Both periods)		— 0.15*	"
Serum cholesterol (6 wks. of age) and			
Serum cholesterol (8 months)		0.13*	"
Body weight (6 wks.)		— 0.09*	"
Adult body weight		— 0.04	"
Age at first egg		0.06	"
Egg production		— 0.02	"
Egg weight (Oct.)		— 0.07	"
" " (March)		— 0.08	"
Specific gravity (Oct.)		0.03	"
" " (March)		0.11	"
Haugh units (Oct.)		— 0.08	"
" " (March)		— 0.01	"
Serum cholesterol (8 mos. of age) and			
Adult body weight		— 0.02	"

Table III. Phenotypic Correlations *(Cont.)*

Correlated Traits	Correlation	Station
Age at first egg	— 0.02	"
Egg production	0.03	"
Egg weight (Oct.)	— 0.13*	"
" " (March)	— 0.13*	"
Specific gravity (Oct.)	0.08	"
" " (March)	— 0.02	"
Haugh units (Oct.)	— 0.24*	"
" " (March)	— 0.22*	"
Shank Score and		
Body weight at 8 weeks (males)	— 0.11	New Hampshire
" " " " (females)	— 0.04	" "
Serum Cholesterol (6 wk.) and		
Body weight at 8 weeks	0.00	Maryland
Adult body weight	— 0.01	"
Age at first egg	0.01	"
Egg production	— 0.06	"
Egg weight (Oct.)	0.02	"
" " (March)	— 0.05	"
Albumen quality	— 0.04	"
Blood spot incidence	— 0.05	"
Meat spot incidence	0.08	"
Shell strength	0.05	"

* $P \leq 0.05$.